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Individual recognition in crayfish (*Cherax dispar*): the roles of strength and experience in deciding aggressive encounters

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The outcomes of agonistic interactions modulate access to resources and thereby affect fitness. Success in agonistic encounters may depend on intrinsic physical and physiological performance, and on social experience. Here we test the hypothesis that previous experience will override physical strength in determining the outcome of fights in the freshwater crayfish *Cherax dispar*. Between unfamiliar opponents, greater chelae closing force significantly increases the chances of winning. However, even when the chelae of the original winners were disabled, the winners kept on winning against the same opponents after 30 min and 24 h. This winner effect disappeared when previous winners encountered unfamiliar individuals. Similarly, a previous loss did not affect the outcomes of subsequent encounters with unknown crayfish. We suggest that this prolonged recognition of individuals and their relative fighting ability is a mechanism that can reduce the number of agonistic encounters experienced by individuals.

Keywords: aggressive behaviour; fitness; winner effect; social dominance; crayfish

1. INTRODUCTION

In animals with dominance hierarchies, agonistic behaviour is an important determinant of fitness (Maynard Smith 1974) and occurs when resources (e.g. shelter, food, mates) are unequally distributed so that dominance over an opponent will result in an immediate benefit for the winner (Parker 1974). Success in agonistic encounters depends on intrinsic factors associated with physical and physiological performance, and on extrinsic factors including social experience (Sneddon *et al.* 1997, 2000*a*; Dugatkin & Earley 2004). Agonistic behaviour is hormonally modulated and the relative concentrations of amines, in particular, are linked to fighting success (Kravitz 1988; Sneddon *et al.* 2000*b*). Additionally, fighting success may depend on usage of ATP via anaerobic metabolic pathways or on the capacity for prolonged oxidative ATP production during extended bouts (Briffa & Elwood 2004; Seebacher & Wilson 2006). Animal size itself will also influence the outcomes of fights (Beauregard *et al.* 1996), even though size does not always translate into physical strength (Seebacher & Wilson 2006).

The effect of physical traits may be modulated by previous experience (Bergman *et al.* 2003; Rutte *et al.* 2006). Hence, animals that have previously lost a fight may be more likely to lose subsequent fights (Chase *et al.* 1994; Dugatkin & Druen 2004). This winner or loser effect may result from social cues that mark winners and losers among conspecifics, or from a self-assessment of an individual's relative fighting ability (Rutte *et al.* 2006).

What is the relationship between intrinsic physical capacity and social experience? If fighting behaviour is dependent on an assessment of the resource-holding potential of opponents (Parker 1974), escalation should be rare and occur primarily between opponents of equal size or strength (Maynard Smith 1974; Earley *et al.* 2003; Davis & Huber 2007). Alternatively, the effect of previous experience may override resource-holding potential.

Here we test the hypothesis that previous experience will override the effect of physical strength in determining the outcome of agonistic encounters. We chose the freshwater crayfish, *Cherax dispar*, as our model organism because the species displays high levels of aggression and engages in agonistic behaviour using their enlarged chelae to hold on to and dislodge their opponents (Wilson *et al.* 2007). We staged fights between familiar and unfamiliar opponents, known winners and losers, and with and without manipulating the closing force of the chelae.

2. MATERIAL AND METHODS

Crayfish (male *C. dispar*, $N=100$; mean total length $=54.2 \pm 0.69$ mm (s.e.)) were collected from wild populations on North Stradbroke Island, Qld, Australia (27°26′ S, 153°36′ E) and taken to Moreton Bay Research Station for experiments. Animals were held separately (one animal per tank) in aerated natural creek water for 24 h before experimentation.

We staged paired encounters in an aquarium ($0.34\times0.20\times0.23$ m) that contained natural creek water and a gravel base of 1 cm. Water temperature was maintained at 23°C, the same as at the collection sites. Two crayfish were introduced simultaneously into the observation tank and the behaviour of each crayfish was observed and recorded over 10 min.

We used a previously developed scoring system (Seebacher & Wilson 2006) to determine the winner of aggressive encounters. The two most prevalent behaviours were 'fights' and 'retreats'. Fights were defined as physical contact between two crayfish during which opponents took hold of each other's chelipeds or chelae and attempted to unbalance each other. Eventually, one contestant would disengage and move away, and the animal remaining was scored as the winner. We quantified a fight as 2 points for the winner. During a retreat, one of the contestants would turn away from the opponent without physical contact, or following contact of the antennae only, and the animal that remained was scored as the winner. We quantified the retreat as 1 point for the winner to reflect the lower intensity of the encounter.

We conducted four experiments, and crayfish were not used repeatedly across experiments. In experiment 1, we tested whether fighting outcomes are repeatable and related to differences in chela force. We staged fights between 10 pairs of crayfish and then restaged the fights after 30 min using the same pairs. In experiment 2, we tested the hypothesis that previous experience of winning or losing within pairs is more important in deciding the outcome of subsequent encounters than relative strength. Following an initial fight ($N=10$ pairs), the chelae of the winners were disabled by attaching the dactylus to the propodus with acrylamide glue. After disabling the chelae, the pairs were made to fight again after 30 min and 24 h.

Experiments 3 and 4 acted as controls. In experiment 3, 30 min and 24 h after an initial fight ($N=10$ pairs), winners of this first fight were competed against unfamiliar crayfish that had no previous experimental winning or losing history. In experiment 4,

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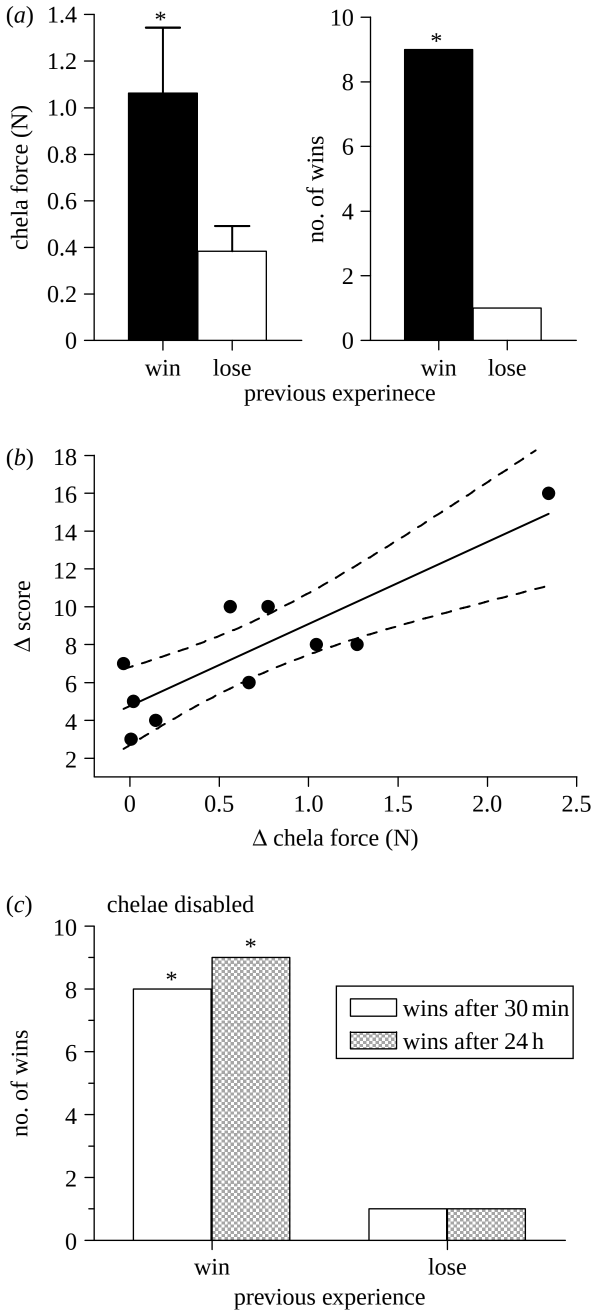

Figure 1. Previous winners won significantly more often when fighting their original opponents after 30 min. (*a*) Winners had significantly greater chela closing force compared with losers, and (*b*) differences in chela force were significantly correlated with differences in the scores between opponents (linear regression line ±95% confidence intervals are shown). (*c*) Even when chelae were disabled, the original winners won significantly more often against their original opponents after 30 min and 24 h. One draw in fights after 30 min was not included in the analysis. An asterisk indicates significant differences between groups of crayfish.

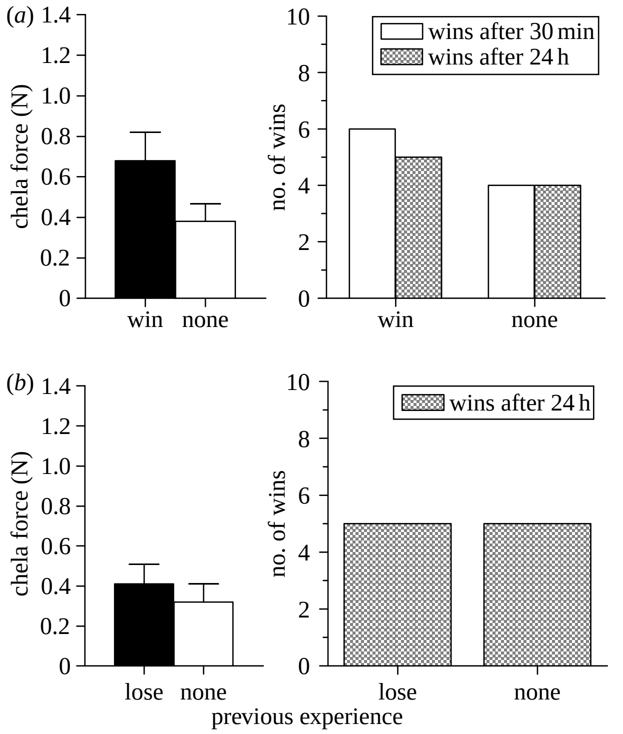

Figure 2. (*a*) Winning a previous fight did not lead to increased success in subsequent fights (after 30 min and 24 h) against unfamiliar opponents with similar chela force. One draw in fights after 30 min was not included in the analysis. (*b*) Similarly, a previous loss did not lead to an increased chance of losing against unfamiliar opponents. Chela force did not differ between opponents in either (*a*) or (*b*).

24 h after their initial fight ($N=10$ pairs), losers were competed against unfamiliar crayfish that had no previous experimental winning or losing history.

All competing pairs were size matched for body length (to within 6% of one another), which was determined using callipers (±0.1 mm). We took digital images of the left and right chelae to analyse size with morphometric software (SigmaScan v. 5.0). For each chela we measured chela length, carpus depth, maximum chela depth, dactylus length, dactylus depth, propodus depth and propodus length. We derived a single measure of mean chela size using principal component (PC) analyses of the morphological measures (Wilson *et al.* in press). We used average PC scores for both chelae for each crayfish as a measure of chelae size, which did not differ between opponents across all experiments (two-sample *t*-tests: all $t_{18}<0.93$, $p>0.36$). All animals were released at their site of capture after experimentation.

Maximum strength of the left and right chelae was measured for each individual crayfish using techniques published elsewhere (Seebacher & Wilson 2006; Wilson *et al.* in press). Total chelae force of crayfish was calculated from the sum of both left and right chelae forces.

Behavioural scores were analysed by χ^2 contingency tables. In each trial ($N=10$ per experiment), winners were determined from their total score (fights+retreats), and for each experiment the null hypothesis was that previous winners, losers or unfamiliar animals will win equal numbers of fights. We compared chelae closing forces by two-sample *t*-tests.

3. RESULTS

In experiment 1, previous winners won significantly more encounters than previous losers during their second fight ($\chi^2=6.4$, $p<0.02$; figure 1*a*). The chela force of winners was significantly greater than that of losers ($t=2.3$, $p<0.04$; figure 1*a*), and the relative score between winners and losers increased significantly with differences in chela force between competitors (linear regression, $R^2=0.74$, $F_{1,8}=22.5$, $p<0.002$; figure 1*b*).

Interestingly, in experiment 2, previous winners also won significantly more fights when repeated after 30 min ($\chi^2=5.4$, $p<0.02$; figure 1*c*) and 24 h ($\chi^2=6.4$, $p<0.02$; figure 1*c*), even though their chelae were disabled. When matched against unknown opponents in experiment 3, however, there were no significant differences in the number of fights won between previous winners and new opponents after 30 min ($\chi^2=0.4$, $p=0.53$; figure 2*a*) or 24 h ($\chi^2=0.1$, $p=0.73$; figure 2*a*), and there were no differences in chela force between the contestants ($t_{18}<1.8$, $p>0.097$). Similarly, when previous losers were matched against unfamiliar opponents, there were no differences between the groups in the number of fights won after 24 h ($\chi^2=0.0$, $p=1.00$; figure 2*b*), and there were no differences in chelae force between groups ($t_{18}=0.65$, $p=0.52$).

4. DISCUSSION

In *C. dispar*, success in winning fights depends initially on strength and subsequently on previous experience with known individuals. Asymmetry in body or weapon size can significantly affect the outcome of fights (Barki *et al.* 1997; Seebacher & Wilson 2006; Wilson *et al.* in press), but it did not contribute to the outcome in our experiments because neither body nor chela size differed between opponents. However, for any given chela size there is considerable variation in the closing force, and this variation plays a significant role in determining the outcomes of fights between similar sized animals. Interestingly, after an initial fight, crayfish retained their status as winners or losers in subsequent fights even when the mechanism facilitating the initial win (i.e. chelae force) was disabled. Hence, resource-holding potential alone does not decide the outcome of fights, rather both experience and physical strength are important. Winner or loser effects are well known in animals (Landau 1951; Oyegbile & Marler 2005; Rutte *et al.* 2006). In *C. dispar*, however, previous winning experience does not increase the chances of future wins against non-familiar individuals, and winner effects exist only among familiar individuals. Similarly, previous losers are not more likely to lose against unfamiliar opponents. Although crustaceans possess the capacity to recognize individual conspecifics (Crook *et al.* 2004; Gherardi & Tiedemann 2004), the persistence of the winner effect for at least 24 h among familiar competitors is remarkable because winner effects are not known to last longer than 60 min (Chase *et al.* 1994; Bergman *et al.* 2003).

Fighting is expensive in terms of energetic costs (Briffa & Elwood 2004) and potential injury (Maynard Smith 1974). Hence, it may be advantageous for individuals (Maynard Smith & Price 1973) to retain information from previous encounters to minimize the number of fights within stable social hierarchies (Berdoy *et al.* 1995). Disturbance to an established hierarchy such as the removal of dominant animals or the immigration of unknown animals may cause the resetting of the 'social experience', requiring renewed aggression to reestablish social positions.

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